VISUALLY MEDIATED RESPONSES IN THE LYCOSID SPIDER
RABIDOSA RABIDA: THE ROLES OF DIFFERENT PAIRS OF EYES

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Video images of conspecifics were presented to *Rabidosa rabida* (Walckenaer) (Araneae: Lycosidae) to study the roles of different pairs of eyes in a wolf spider. Four groups of spiders had one pair of eyes occluded, and four had all but one pair occluded. Various control groups were also tested. The PLE were essential for sizeable orientation turns of up to about 160°. The PME served for rapid, long distance approaches toward the stimulus; they also initiated orientation turns of up to about 50°. If close to the stimulus, the ALE initiated small turns of up to about 20° and mediated small approaches. The AME did not mediate any responses. Courtship could be triggered in males via the PLE or the PME. In females, only the PME mediated receptive display responses to temporally patterned leg I movements seen in anterior or lateral views of a courting male. □*Araneae, Lycosidae, eyes, vision, communication.*

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Very little behavioural research has been carried out on vision in lycosid spiders, compared to the extensive studies on salticid spiders (reviewed in Forster, 1985). In lycosid spiders, occlusion of the eyes has been used to test for differences in the roles of the main vs. secondary eyes (Homann, 1931) as well as the anterior vs. posterior eyes (Acosta *et al.*, 1982); however, the results of both of these studies were confounded by the lack of controls for vibratory stimuli. The only successful behavioural investigation of the role of particular eyes in lycosids (Magni *et al.*, 1964) demonstrated the importance of the AME in astronomical orientation and was accomplished by covering all but a single pair of eyes in each group tested. Occlusion of only one pair of eyes at a time has proven useful in several behavioural studies of salticid vision (e.g., Forster, 1979).

In the present study of the lycosid spider *Rabidosa rabida* (Walckenaer), I used both methods of occlusion to examine the roles of different pairs of eyes in detecting visual stimuli and mediating appropriate responses. By using video images as stimuli (Clark and Uetz, 1990), I eliminated the possibility that vibrations or chemicals from conspecifics could confound the results.

METHODS AND MATERIALS

Penultimate *Rabidosa rabida* (formerly *Lycosa rabida*) were collected in late June (1990 and 1991) in Athens County, Ohio, USA. The methods of maintenance and the laboratory conditions during testing have been described previously (Rovner, 1989). Spiders were not used in testing until 1 week after the final moult. Tests were conducted between 1000 and 2200 hours.

For each test the spider's home cage, with its resident within, was placed with its narrow front side facing a small television set (black and white Magnavox BH-3907; screen = 9.2cm wide, 6.6cm high), which received a playback signal from a Sony recorder (SL-HFR70). The clear front side of the plastic cage (the other sides were opaque) was 7cm wide and was located 3cm from the screen. I removed the cage cover and, if necessary, gently positioned the spider with an artist brush to insure that the screen would be within the visual field of the spider's useable eyes. (I used separate brushes for males and females). Then, a glass cover (one for each sex) was placed on top of the cage. A front-silvered mirror fixed at 45° to the floor was 0.5m above the cage. A video camera (JVC GX-8NU) was aimed at both the mirror and an adjacent, second, identical television set receiving the same signal from the playback recorder as the first set. Thus yielded (on a second, identical recorder) a kind of split-screen recording. On the left was a dorsal view of the spider, which facilitated the measurement of turning angles (accurate to the nearest 5°) and speeds of locomotion. On the right was a view of the video image concurrently being presented to the spider. Thus, the relationship of

the video stimulus to the spider's response could later be analyzed.

Subjects used for video presentations were recorded against a plain, pale background and illuminated evenly by a 32-W, circular fluorescent bulb 0.5m above the arena. The camera was located at a distance yielding a screen image the size of the actual subject (average body lengths: female=18mm; male=12mm). The 15-min video playback for females was a pheromone-stimulated, courting male; his occasional position changes provided nearly equal proportions of anterior and lateral views of his display (total number of courtship bouts = 51). The 10-min video playback for males was a lateral view of a female walking to and fro in an elongate glass arena (passes across the screen =15 leftward and 15 rightward). Some preliminary tests made use of prey images provided by a 10-min video of three crickets (*Acheta domesticus*, 10mm body length) walking to and fro.

To cover the eyes of spiders, I painted them with two coats of water-based enamel (Top Color Hobbylack, Pelikan AG). That this insured complete occlusion had been established previously (Rovner, 1989). Spiders were tested one or more days later.

I ran two preliminary tests to see if painting or its related procedures lowered responsiveness. All the eyes of five females were covered with two separately applied coats of clear paint. Five other females were briefly anaesthetised (carbon dioxide) and then restrained for 6 hr, thereby duplicating the procedure used when painting the eyes. However, at the two times that paint would have been applied (0 hr and +3 hr), I used water instead. The next day, when exposed to video images of crickets, the clear-painted spiders were less responsive than were the water-brushed spiders. The latter seemed as responsive as untreated spiders.

There were three control groups, each with 10 females and 10 males; these 60 individuals were given two trials apiece. One group consisted of untreated spiders exposed to the conspecific video playback, to determine how readily fully sighted spiders respond. A second group, also untreated, was exposed to a 10-min video of an empty arena, to determine if that alone had a stimulating effect. (Light from the screen = about 800 lux; incident light from above = about 350 lux.). The third group consisted of fully blinded spiders exposed to the conspecific playback, to see if such spiders would perform behaviours (orientation, rapid approach, or display) that I

assumed would only occur in this study as visual responses.

There were eight experimental groups, each having 10 spiders of each sex. In four experimental groups a single pair of eyes was occluded; in four others, all but one pair was occluded. Since one of the untreated control spiders had failed to respond to video playback within two trials and since the preliminary tests had indicated that painting the eyes can reduce responsiveness, I gave unresponsive experimental spiders additional opportunities to respond, up to a limit of five trials. One or more days separated consecutive trials undergone by any individual spider.

RESULTS

During testing of control groups, all of the untreated females and all but one of the untreated males showed 'orientation' and/or 'long-range approach.' Most (16/20) did so in the first trial. 'Orientation' involved a single, rapid pivot that resulted in the spider facing the image. This pivot had a mean speed (SD) of $121 \pm 51.7°$/s ($N = 12$), about eight times faster than turns that occurred during wandering, $16 \pm 12.4°$/s ($N = 11$). A 'long-range approach' covered a distance of up to 10cm, the maximum being limited by cage depth (12.5cm). The speed of an approach, 5.9 ± 3.32 cm/s ($N = 22$), was about ten times faster than walking during wandering, 0.6 ± 0.31cm/s ($N = 36$). (The above speeds are not the maxima attained, since I included the acceleration and deceleration phases in each bout of locomotion.) No orientation or approach responses occurred in the empty arena or fully blind controls.

Results of the eye occlusion experiments are summarized in Table 1. Spiders with any one of the four pairs of eyes occluded were still capable of orientation; those with occluded PME did not show approach. When all but one pair of eyes was occluded, the only group failing to show orientation was the one limited to use of the AME; and the only group that still showed long-range approach was the one with useable PME. When close to the cage front, a few spiders having only useable ALE did perform a near-field approach response, edging forward less than one body length. For all the responding experimental groups, the mean number of trials ($\pm$ SD) needed to obtain either an orientation or a long-range approach to the image was 1.2 ± 0.53 ($N = 63$) for females and 2.4 ± 1.24 ($N = 55$) for males (Mann-Whitney U-test, $Z = -6.545$, $P<0.0001$).

Spiders with useable PLE showed orientation

Condition	Orientation		Long range approach		Display	
	♀	♂	♀	♂	♀	♂
Untreated	6	6	8	7	3	5
Empty arena	0	0	0	0	0	0
Fully blind	0	0	0	0	0	0
No PLEs	6	7	10	4	5	3
No PMEs	10	6	0	0	0	4
No ALEs	10	7	9	5	4	4
No AMEs	10	6	9	6	4	3
Only PLEs	10	7	0	0	0	5
Only PMEs	9	6	10	5	5	2
Only ALEs	3	1	0	0	0	0
Only AMEs	0	0	0	0	0	0

TABLE 1. Number of ♀ and ♂ spiders responding to video playback. $N = 10$ spiders/sex/condition. Each spider was allowed more than one trial to respond: controls, up to two trials; experimentals, up to five trials. Only ♂♂ that also performed orientation or approach are included under 'Display'.

turns of up to about 160°. Those with only the PME useable performed orientation turns of up to about 50°. If near the stimulus, those with only the ALE useable showed orientation turns of up to about 20°.

During playback of male courtship, only those females with non-occluded PME performed leg-waving receptive displays (Table 1). This brief display occurred 3.0 ± 1.9s ($N = 30$) after the abrupt termination of the male's courtship bout. The receptive display was sometimes performed unimpeded, this being the case in females which had not yet reached the front of the cage. However, it was usually constrained, since most females quickly approached the cage front and rested their anterior legs against the wall. Still, the timing of their response remained precise. Females showed this display while seeing anterior or lateral views of the courting male.

Up to 6/10 of the males tested in each condition performed courtship display, which occurred in every group. It even occurred in two males during the empty arena playback and in three of the fully blinded males, such data reflecting a previously noted readiness of R. rabida to sometimes court in response to subnormal stimuli (Rovner, 1968). Perhaps these non-visually stimulated courtships were triggered by mechanical cues resulting from my moving the cage to the testing site or from my positioning the spider with a brush (to duplicate the procedure used on experimental spiders). For this reason, only courtships occurring during trials in which orientation or approach also occurred were scored as visually initiated displays. (This

may have prevented some visually stimulated males that were facing the stimulus at the outset from being included in the courtship total for some experimental groups.) Only males with use-able PLE or PME showed courtship accompanied by orientation, and only males with non-occluded PME showed courtship accompanied by approach (Table 1).

DISCUSSION

Data presented here indicate that R. rabida's posterior eyes play major roles in mediating responses to important visual stimuli, as was earlier predicted for lycosids on anatomical grounds (Homann, 1931; Land, 1981). The PLE serve the same function that they do in salticid spiders, that of detecting stimuli in an extensive visual field and initiating the largest orientation turns. They cannot mediate approach behaviour. On the other hand, the PME are essential for mediating rapid, long-range approaches to stimuli. They can also initiate orientation turns of up to 50°.

As to the anterior eyes, at close range the ALE can play small roles in orientation and approach. This contradicts Land's (1981) suggestion that only the large posterior eyes are involved in prey capture. As predicted for lycosids by Land (ibid.), the AME of R. rabida play no role by themselves in mediating turns or approaches toward a target. Whether they serve for other than polarized light detection (Magni et al., 1964) remains to be explored.

The present findings on the anterior eyes of R. rabida may not apply to all lycosids. For example, unlike R. rabida, in Arctosa variana the AME are larger than the ALE (ibid.). Also, local tiering is found in the retinae of the AME of Geolycosa godeffroyi but not in the type genus Lycosa (Blest and O'Carroll, 1989). Furthermore, the finding of high nocturnal sensitivity in the anterior eyes of Lycosa tarentula (Carricaburu et al., 1990) suggests that an understanding of the capabilities of the anterior eyes of lycosids will require examining different species under various illumination conditions. Finally, I must point out that I did not test for any possible collaboration between different pairs of eyes. Collaborative visual mechanisms were revealed in salticid spiders by ipsilateral blinding (Forster, 1979).

As in the salticids (Forster, 1985), orientation and approach are the initial behavioural responses of lycosid spiders to moving images, whether prey or mating partners. Thus, the performance of such behaviours does not specify the spider's

motivational state. However, the fact that twice as many trials were needed to obtain these behaviours in males as in females suggests that such initial responses relate primarily to predation, i.e., that adult females, on average being hungrier than males, are more responsive to visual stimulation. A subsequent occurrence of display behaviour indicates a switch to sexual motivation.

For display to occur in females the PME have to be useable, and they are sufficient by themselves for mediating this response. The fact that lateral as well as anterior views of the courting male elicited responses suggests that the cue is movement of the male's black leg I: it extends forward in a pumping-like motion of increasing frequency and then abruptly flexes back. Unlike salticid face-to-face courtship, in which the perceived form of the male may be as important for the female as his behaviour (*ibid.*), female *R. rabida* need not view the male's anterior. Apparently, detection of a temporal pattern of movement suffices for recognition.

As to visually-triggered courtship display, male *R. rabida* differ from male salticids, which require one particular pair of eyes, the AME (*ibid.*). Stimulation of either pair of a male *R. rabida*'s posterior eyes suffices for triggering courtship. If the PLE are involved, orientation precedes display. If the PME are involved, approach can precede display, although it need not do so.

Given that the movement-detecting PLE are sufficient for courtship onset in *R. rabida*, an adequate stimulus in this species may be any object of an appropriate size, speed, and perhaps movement pattern entering the extensive visual field of the PLE. Since the other three pairs of lycosid eyes are also assumed to be movement detectors (Land, 1981), there may be no need to require their involvement in additional visual analysis before initiating courtship. However, this may not be true for all lycosids. In particular, female *Pardosa laura* have been hypothesized to use form vision for species discrimination (Suwa, 1984). If male *P. laura* likewise do so, eyes other than the PLE would be have to be used for such form analysis in order to inititate courtship.

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